

Ecology and Evolution

Open Access

Parrots as key multilinkers in ecosystem structure and functioning

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Keywords

Ecosystem structure and dynamics, mutualistic functions, Psittaciformes, vertebrate frugivores.

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Funding Information

Funding was provided by Zoo de Barcelona and Biorena (January 2011), Junta de Andalucía (PAI RNM107 to JLT and FH, April–September 2011), Fundación Biodiversidad (2012–2013), Fundación Repsol, and a Severo Ochoa award (to FH).

Received: 31 March 2015; Revised: 19 July 2015; Accepted: 25 July 2015

***Ecology and Evolution* 2015; 5(18): 4141–4160**

doi: 10.1002/ece3.1663

Abstract

Mutually enhancing organisms can become reciprocal determinants of their distribution, abundance, and demography and thus influence ecosystem structure and dynamics. In addition to the prevailing view of parrots (Psittaciformes) as plant antagonists, we assessed whether they can act as plant mutualists in the dry tropical forest of the Bolivian inter-Andean valleys, an ecosystem particularly poor in vertebrate frugivores other than parrots (nine species). We hypothesised that if interactions between parrots and their food plants evolved as primarily or facultatively mutualistic, selection should have acted to maximize the strength of their interactions by increasing the amount and variety of resources and services involved in particular pairwise and community-wide interaction contexts. Food plants showed different growth habits across a wide phylogenetic spectrum, implying that parrots behave as super-generalists exploiting resources differing in phenology, type, biomass, and rewards from a high diversity of plants (113 species from 38 families). Through their feeding activities, parrots provided multiple services acting as genetic linkers, seed facilitators for secondary dispersers, and plant protectors, and therefore can be considered key mutualists with a pervasive impact on plant assemblages. The number of complementary and redundant mutualistic functions provided by parrots to each plant species was positively related to the number of different kinds of food extracted from them. These mutually enhancing interactions were reflected in species-level properties (e.g., biomass or dominance) of both partners, as a likely consequence of the temporal convergence of eco-(co)evolutionary dynamics shaping the ongoing structure and organization of the ecosystem. A full assessment of the, thus far largely overlooked, parrot–plant mutualisms and other ecological linkages could change the current perception of the role of parrots in the structure, organization, and functioning of ecosystems.

Introduction

Current theory predicts that if pairwise relationships between organisms have evolved as mutualistic, selection should have acted to maximize the probability of interaction between partners (Bronstein 1994; Thompson 1994). In addition to the evolution of particular adaptations, these mutually enhancing interactions may also drive the properties and functioning of ecological systems through the temporal convergence of eco-(co)evolutionary dynamics (Thompson 2005; Fussman et al. 2007; Guimarães

et al. 2011; Nuismer et al. 2013), whose effects may be contemporarily, albeit partially, observed in the makeup of present-day ecosystems (Loreau 2010; Schoener 2011; Wisz et al. 2013). Therefore, empirical approaches that address the influence of plant–animal mutualistic interactions to explain species-level properties (e.g., abundance or dominance) of interacting partners in ecological communities can be crucial to understanding ecosystem structure and functioning.

It has been extensively argued that vertebrate frugivores are important functional components of ecosystems

making a central contribution to seed dispersal (Fleming and Kress 2013). By enhancing the demography of their food plants, frugivores can influence the composition and abundance of plant communities, as well as those of other organisms acting as secondary dispersers, thus playing a clear role in ecosystem structure and functioning (Wisz *et al.* 2013). Mutual benefits for frugivores and their food plants have often been inferred on the assumption that seeds should be swallowed and subsequently defecated or regurgitated in order to be efficiently dispersed (Fleming and Kress 2013). Although many animals reduce the number of diaspores by consuming them, they can still benefit food plants by directly promoting genetic flow by endozoochorous seed dispersal and pollination, by alternative seed dispersal methods, by facilitating seed removal by secondary seed dispersers, and by other processes such as protective interactions (Norconk *et al.* 1998; Vander Wall *et al.* 2005). However, the study of plant resource–animal service mutualisms has often focused on particular pairwise interactions between individual partners or groups of species providing single services to their food plants, mainly on fully mutualistic pollination and endozoochorous seed dispersal services (Fleming and Kress 2013). Much less attention has been devoted to different services provided simultaneously or at variable spatiotemporal scales and life stages by particular mutualists to multiple plant species. These “keystone mutualists” (Gilbert 1980) or “super-mutualists” are expected to be trophic generalists with a potentially pervasive impact on the vital cycles of their food plants and other organisms, and with wide implications for populations and communities.

Parrots (Psittaciformes) are trophic generalists and constitute rich species guilds, accounting for a high density and biomass, in many tropical and subtropical ecosystems (Terborgh *et al.* 1990; Collar 1997). They exhibit a greater range of size, morphology, and foraging behaviors than other groups of frugivorous vertebrates; this often implies a variety of exploited parts from a high diversity of plants, high visitation frequency to food plants, and large numbers of items handled per feeding bout or time unit, including flowers, fruits, and seeds that are bitten, wasted, carried in the beak, masticated, and swallowed (Collar 1997; Juniper and Parr 2010). Although many studies indicate that parrots behave as trophic generalists (e.g., Ragusa-Netto and Fecchio 2006; Gilardi and Toft 2012; Lee *et al.* 2014), several patterns have been found, suggesting that larger species tend to feed more on seeds, while smaller species fed more on fruit flesh (Matuzak *et al.* 2008). Smaller parrot species have also been found to consume mainly small, soft fruits, whereas larger species can consume both hard and soft fruits (Rowley *et al.* 1989; Galetti 1997). Moreover, some parrots are also

known to prey on plant-eating invertebrates (Collar 1997; Juniper and Parr 2010). Despite this widespread range of interactions with their food plants, parrots are generally considered plant antagonists and “cheaters” in effective plant–animal mutualisms. This view is based mainly on the assumption that they obtain nutritional rewards by reducing the fitness of their food plants without any compensation in the form of functional services. For instance, they have repeatedly been deemed harmful predispersal seed feeders and thus ineffective or illegitimate seed dispersers (e.g., Janzen 1981; Haugaasen 2008; Gilardi and Toft 2012). This is because they presumably do not regurgitate or defecate viable seeds but generally destroy them as do other “pure seed exploiters” such as granivorous birds, rodents, and ruminants. However, most seed predators have been shown to eventually act as facultative primary and secondary dispersers (Norconk *et al.* 1998; Vander Wall *et al.* 2005; Heleno *et al.* 2011). Thus, except for the role of brush-tongued lorikeets (Loriinae) as major avian pollinators in the Australasian region, parrots have been generally neglected as forming part of a mutualistic network in the evolution and coevolution of vertebrate frugivores and their food plants (Fleming and Kress 2013).

Although parrots undoubtedly act as plant predators, recent works suggest that at least some parrots species may also provide key mutualistic services through endozoochorous (Oliveira *et al.* 2012; Young *et al.* 2012) and estomatochorous seed dispersal (Tella *et al.* 2015) and that whole seeds wasted by parrots (Symes and Perrin 2003) may be available for secondary seed dispersers. These behaviors may have simply been overlooked by researchers given the generalized view of parrots as pure plant antagonists (Tella *et al.* 2015). Moreover, the role of frugivores as antagonists or mutualists is often context dependent regarding the plant species, the part of the plant used, the time of year, fruiting abundance, presence and abundance of competitors and predators, and, importantly, the underlying abiotic influences behind most of these factors (Price *et al.* 1980; Jordano 2000; Schupp *et al.* 2010; Fleming and Kress 2013). In addition, plant antagonists can influence the demography of their food plants and hence the composition and abundance of vegetal communities (Dirzo and Miranda 1991). This influence has been traditionally associated with the active preference or avoidance of food according to their nutritional features and palatability due to the chemical and physical defences used by plants to avoid predation (Dearing *et al.* 2005). The nutritional features and chemical compounds used as frugivore deterrents by plants can vary spatiotemporally, and among species and individual plants (Iason *et al.* 2012). Likewise, vertebrate frugivores can show variable nutritional requirements and resistance

to chemical plant defences (Karasov and Martínez del Río 2007), often making it difficult to disentangle their role as mutualists and/or antagonists (Tewksbury 2002).

In this study, we aimed to assess the potential role of parrots as linkers for several ecological processes through the annual parrot and plant cycles in a particular ecosystem, the dry tropical forest of the Bolivian inter-Andean valleys. This ecosystem has been shown to have lower avian frugivore richness than expected from overall bird diversity (Kissling *et al.* 2009), and thus, we expected a relevant role for parrots despite the fact that they are generally not considered as plant mutualists. To assess the functional importance of the parrot guild, we quantified the abundance, density, and biomass contribution of each parrot species in the community of avian frugivores and evaluated whether their food plants represent a major proportion of the dominant woody plants. In order to test whether parrots provided diverse services to their food plants, we assessed whether the form of feeding on and wasting of each plant structure contributes to driving particular stages of plant life cycles. We hypothesised that if interactions between parrots and their food plants evolved as primarily or facultatively mutualistic, selection should have acted to maximize the strength of their interactions by increasing the amount and variety of resources and services involved in particular pairwise and community-wide interaction contexts. This “super-mutualist hypothesis” extends the implications of the “abundance hypothesis”, postulating that interaction frequencies between species depend on their functional interdependence (reviewed by Vázquez *et al.* 2009), to predict that plants providing more types of food resources exploited by their mutualistic consumers should be those in turn receiving more services from them. In addition, if mutually enhancing relationships have been favoured in this interaction system, both plant and parrot species reciprocally providing and receiving more resources and services from their mutualist partners should be numerical, functional, or biomass dominant in ecological assemblages (Keddy 1992; Wisz *et al.* 2013). These predictions rely on the assumption that species-level traits are central biological properties pervading not only the interaction complex but, importantly, also the outcomes on the ecosystem structure of the eco-(co)evolutionary process (Strauss and Irwin 2004; Smallegange and Coulson 2013).

Methods

Study area and species

The study area covers the whole tropical dry forest biome of the inter-Andean valleys of Bolivia. The area covered

in this study is located on the eastern slopes of the central Bolivian Andes and includes areas in the departments of Santa Cruz, Cochabamba, Chuquisaca, and Potosí, around Mizque, Caine, Grande, and Pilcomayo Rivers, at altitudes ranging from 900 to 3500 m (18°6' S, 64° 35' W, see location map in Tella *et al.* 2013). The climate ranges from dry to semi-arid with rainfall generally oscillating between 200 and 650 mm concentrated in the austral summer. The habitat is a tropical dry forest that has been transformed by long-term human activities to thorn and cactus scrub with scattered trees and crops (Navarro and Maldonado 2002). The vegetation is not well characterized, but includes at least about 2000 species with a high proportion (about 18%) of endemism (Navarro and Maldonado 2002; López 2003; Atahuachi-Burgos *et al.* 2005). Most of our sampling was carried out over an area of about 25,000 km² (see Tella *et al.* 2013), encompassing the full range of habitats, including dry forest and thorny scrubland mixed in differing degrees with cultivations and pastures, both on hillsides and valley bottoms with vegetation associated with temporary or permanent water courses (Atahuachi-Burgos *et al.* 2005).

The study focuses on the nine parrot species that can be regularly observed in the study area (Table 1, Fig. 1). Among them, *Ara rubrogenys*, *Myiopsitta luchi*, and the subspecies *Thectocercus acuticaudatus neumanni* and *Pyrhura molinae molinae* are endemic to the study area. One species (*Aratinga leucophthalmus*) observed on a single occasion was excluded from the analysis. Other rare parrot species (*Ara militaris*, *Amazona tucumana*) have been recorded occasionally in the study area, moving from the neighboring montane and Yungas forests, but were not recorded in the present study.

Parrot surveys, detection probabilities and density estimates

Data were collected during eight surveys conducted between January 2011 and November 2013; four surveys were conducted in the parrot breeding season (rainy season: December–April) and four in the nonbreeding season (dry season: May–November). This involved 153 full days of field work by 2–5 people, totaling 401 person-days. We drove slowly (20–40 km/h) through unpaved roads avoiding the central hours of the day, when the activity of parrots is reduced (Tella *et al.* 2013). When parrots were located, stops were made to record the number and species of parrots, and when it was possible the distance at which they were first detected using laser rangefinders incorporated into binoculars. Abundance was estimated as the total number of individuals counted across transects (totaling 6823 km), and transformed to number of individuals per kilometer of transects. We also recorded

Table 1. Total count represents the number of individuals of each species counted in the transects. Relative abundance (individuals/km) was defined as the number of parrots and other large avian frugivores per kilometer of transects (6823 km). Parrot density (individuals/10 ha) was calculated by dividing the species-specific detectability-corrected estimates of abundance by the area effectively surveyed (see Appendix S1). Parrot biomass (kg/km²) was calculated by multiplying the density by the average body mass of each species. Species strength was calculated as the sum of the relative frequencies of each parrot species interaction (number of foraging individuals) with the set of their food plants. The number of plant parts from each exploited plant species was summed to define an interaction index for each parrot species, expressed as Trophic Interactions, while the number of mutualistic functions provided by each parrot species to their food plants was expressed as Mutualistic Interactions.

Species	Total count	Relative abundance	Density	Biomass	Feeding bouts (individuals)	Plant species	Species strength ¹	Trophic interactions/Mutualistic interactions ¹
Parrots (Psittaciformes)								
<i>Ara rubrogenys</i> (550 g)	1890	0.277	0.051	2.805	217 (2499)	19	4.38	28/11
<i>Thectocercus acuticaudatus</i> (165 g)	8243	1.208	0.528	8.712	445 (5386)	52	23.45	108/41
<i>Aratinga leucophthalmus</i> (155 g) ²	12	0.004	–	–	1 (12)	1	–	2/0
<i>Psittacara mitratus</i> (220 g)	4520	0.662	0.178	3.916	167 (4277)	27	13.24	52/17
<i>Myopsitta luchi</i> (134 g)	5447	0.798	0.583	7.812	211 (4765)	32	16.14	67/18
<i>Pyrrhura molinae</i> (70 g)	234	0.034	0.024	0.168	31 (252)	16	1.88	33/6
<i>Psilopsiagon aymara</i> (45 g)	817	0.119	0.151	0.679	97 (923)	39	25.48	52/5
<i>Brotogeris chiriri</i> (72 g)	2398	0.351	0.198	1.426	79 (1279)	19	4.74	35/11
<i>Pionus maximiliani</i> (263 g)	97	0.014	0.006	0.158	21 (157)	7	2.03	8/2
<i>Amazona aestiva</i> (475 g)	816	0.119	0.033	1.568	90 (2737)	26	8.65	50/21
Total parrots	24,474	3.587	1.752	27.244	1359 (22,287)	113		433/132
Other large frugivorous birds								
Tinamous (Tinamidae)								
<i>Cryptorellus tataupa</i> (221 g)	2	0.0006						
Guans (Cracidae)								
<i>Penelope obscura</i> (1080 g)	14	0.002						

¹Excluding cultivated herbs and exotic plants.

²Accidental species not included in the analysis.

the relative abundance (individuals/km) of other large recognized avian frugivores, that is, tinamous (Tinamidae) and guans (Cracidae) present in the ecosystem. Other large-bodied recognized frugivores able to ingest or transport relatively large (>5 mm diameter) seeds by other methods (e.g., monkeys, trogons, toucans, cotingas) were not present in the ecosystem, while facultative frugivores (e.g., Greater grison, *Galictis vittata*, Crab-eating fox, *Cerdocyon thous*) and scatter-hoarding rodents (e.g., Common yellow-toothed cavy, *Galea musteloides*) occurred at comparatively much lower abundances (Anderson 1997, pers. obs.). However, the latter were not adequately recorded or quantified due to logistic and time constraints derived from their nocturnal and elusive habits. No observation of frugivorous bats was recorded, but their role as dispersers cannot be discarded. Smaller, partially frugivorous birds were mainly fruit mashers and gupers from the Turdidae, Thraupidae, Cardinalidae, and Fringillidae families. During the feeding observations of parrots, these smaller frugivores were rarely recorded swallowing entire fruits, predating on their seeds (e.g., Black-backed grosbeak, *Pheucticus aureoventris*, Cardinalidae, feeding on seeds of *Tipuana tipu*), or feeding on the pulp of fruits with tiny seeds that could be ingested

intact. However, this study was not designed to assess frugivory in these species.

To account for detection error and correct for variable detectability among species in field counts (Dénés *et al.* 2015), we estimated the average individual detection probability (P) for each species by fitting detection functions with a hierarchical distance-sampling model for line transect data (Royle *et al.* 2004) using the *unmarked* package (Fiske and Chandler 2011) for program R (R Core Team 2014). We expected that detection would decrease monotonically with distance from the survey line (x) and modeled this process using the half-normal detection function, $g(x) = \exp(-x^2/2\sigma^2)$, where σ is the half-normal scale parameter. Distances were recorded on a continuous scale, but after exploratory analysis, we decided to group them into distance classes to facilitate fitting of the detection function. Following recommendations in Buckland *et al.* (2001) for line transect distance sampling, we defined maximum detection distances limits (right truncation) for each species (w_{sp}) by excluding the 5% farthest detections and continued the analysis with the data from the remaining 95% records. We derived the detection probability within the surveyed strip by integrating $g(x; \sigma)$ over the maximum perpendicular distance (x_{max}):

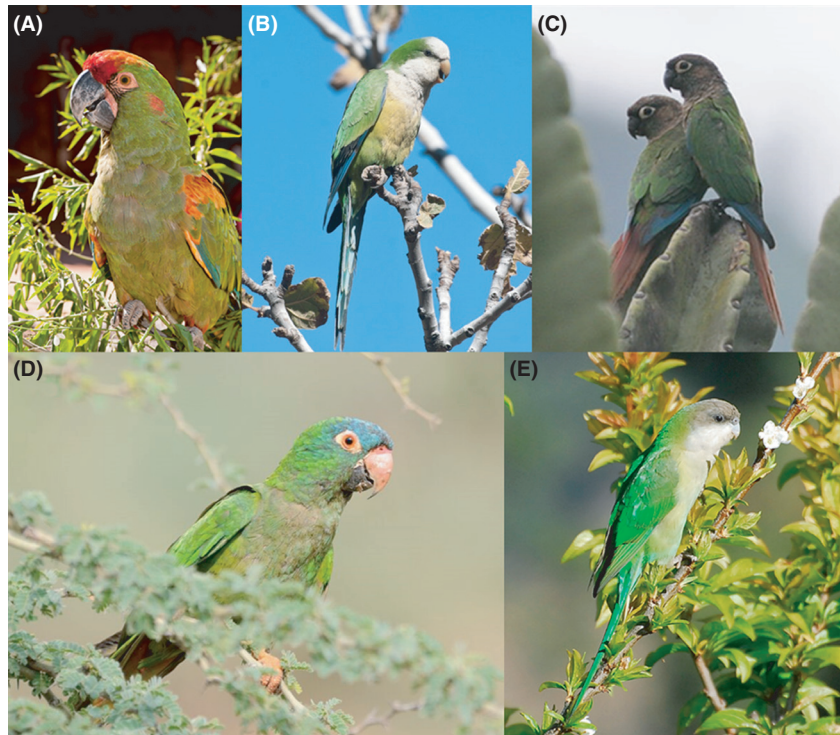


Figure 1. Endemic parrot species (A) *Ara rubrogenys* and (B) *Myiopsitta luchi*; subspecies (C) *Pyrrhura molinae molinae* and (D) *Thectocercus acuticaudatus neumanni*; and the smallest species (E) *Psilopsiagon aymara* in the parrot community from the Bolivian inter-Andean valleys. Photographs by Héctor Garrido (A, B), Manuel de la Riva (C, D), and José L. Tella (E).

$$p = \frac{\int_{x_{\min}}^{x_{\max}} g(x; \sigma) dx}{x_{\max}}$$

Data on number of detections, the 95% maximum detection distances (w_{sp}) used for each species, and the estimated detection probabilities with 95% confidence intervals are shown in Table S1 and Fig. S1.

Detectability-corrected estimates of abundance for each species were obtained by dividing the total counts by p (Table 1). Parrot densities were calculated by dividing the detectability-corrected estimates of abundance by the area surveyed [$\text{individuals}/(\text{km}_{\text{transects}} \cdot 2w_{sp})$]. Parrot biomass (kg/km^2) was calculated by multiplying the density by the average body mass of each species obtained from Forshaw (2006).

Vegetation surveys

Multiple surveys ($n = 70$) were conducted on both sides of unpaved roads throughout the study area, covering all types of vegetation during the rainy ($n = 39$ surveys) and dry ($n = 31$ surveys) seasons, to collect information on forest structure and composition, slope orientation, altitude, microhabitat (e.g., presence of water courses, soil composition, etc.), and on the presence, relative abundance, and flowering and fruiting phenology of woody plants. Survey plots were of variable size (ranging from 2 to 10 km) depending on the complexity of the vegetal

communities, which decreased with altitude (Navarro and Maldonado 2002; López 2003). Phenology was recorded by including each individual plant in one of the following categories: (1) without reproductive activity, (2) with flowers, (3) with flowers and unripe fruits, (4) with unripe fruits, (5) with ripe and unripe fruits, and (6) with flowers, ripe, and unripe fruits. Overall, plant phenology was recorded on 20 individual plants per sampled species, totaling 1017 recordings on >20,000 individual plants. We recorded the above information on the dominant plants in each survey, ranging from 2 to 33 plant species per survey (mean \pm SD = 14 ± 7). This information was complemented with that from the literature (Jardim et al. 2003; Atahuachi-Burgos et al. 2005) to create a composite index of overall “dominance” for each woody plant species present in the ecosystem, hereafter “plant dominance index”. This index was computed as the rating sum of the categorical levels assigned to four variables recorded for each species, regarding (1) distribution range with five levels considering frequency of occurrence in the surveys and slope orientation, as this factor greatly determines species distribution in the study area (Navarro and Maldonado 2002; López 2003); (2) altitude, with three levels increasing from narrow to wide range between 1000 and 3000 m; (3) habitat requirements, with two wide levels corresponding to species with specific microhabitat requirements regarding soil composition, humidity, etc., and those generalist species without clear specific microhabitat requirements; and (4) relative abundance with

three wide levels ranging between a relict presence and a high abundance where present (Table S2). Therefore, plant dominance was widely defined as the combined contribution to ecosystem shaping of distribution range, environmental requirements (niche breadth), and relative abundance of each plant species.

Foraging observations

When parrots were observed foraging, their number, food handling behavior, and the consumed part of each plant species were recorded, both within and outside transects conducted to determine their abundance. In the case of fruits, we noted whether parrots handled and consumed pulp of ripe or unripe fruits and their mature or immature seeds, respectively, and whether parrots dropped each food type beneath the canopy of food plants. The diameter of the smallest and largest axis (measured with callipers to the nearest mm) of a sample of ripe fruits and their seeds, as well as the number of seeds per fruit, was recorded in the field. After each feeding observation, we attempted to confirm what parrots were eating and wasting by searching for food remains on the ground beneath foraging sites.

When foraging parrots were observed departing from food plants with fruits in the beak or feet, we followed them visually with binoculars to attempt to determine whether they dropped ripe fruits and defleshed mature seeds during flight or at subsequent stopovers at foraging and perching sites. We measured the approximate distances moved from the mother plant with a laser range-finder incorporated into the binoculars (see Tella et al. 2015). Some distances recorded should be considered conservative estimates when flying parrots were out of sight in the forest while transporting fruits or seeds.

To determine whether the fruit-wasting behavior of parrots (e.g., Symes and Perrin 2003) facilitated the availability of seeds and other plant structures used as food by secondary seed dispersers and other organisms, we recorded the presence and abundance of entire ripe fruits, intact mature seeds separated from the pulp, and other vegetable matter dropped by parrots beneath the canopy of food plants. The identity of potential secondary dispersers was opportunistically recorded by direct observation and by recording the presence of feces containing seeds beneath and at a short distance from parent plants.

Foraging interactions

The quantitative importance of each parrot species to the community of their food plants, and vice versa, defined as species strength (*sensu* Bascompte et al. 2006), was calculated as the sum of the relative frequencies of each parrot species interaction (number of foraging individuals) with

the set of their food plants independently of the plant part and structure on which parrots fed. Species strength from the plant's perspective was computed as the sum of the relative frequencies of each plant species interaction with the parrot community.

Flocking parrots can eat different plant parts (e.g., ripe and unripe fruits) on single or neighboring individual plants, both simultaneously by different individuals or sequentially by particular individuals, making it difficult to quantitatively determine the number of parrots consuming each plant part in each foraging bout. Therefore, we focused on the qualitative determination of the number of different parts consumed during particular foraging bouts. To assess the qualitative extent of the foraging interactions between parrots and their food plants, we summed the number of different parts (p) of each plant species (s) that each parrot species (x) consumed considering all observations as a whole. We categorized the used plant parts as (p_1) ripe fruits, (p_2) unripe fruits, (p_3) mature seeds, (p_4) immature seeds, (p_5) pollen, (p_6) nectar, (p_7) flower buds, (p_8) other mature flower structures, (p_9) bark, (p_{10}) gum, (p_{11}) sprouts and leaves, (p_{12}) leaf tying invertebrates, and (p_{13}) other invertebrate plant antagonists. With these data, we computed (1) a qualitative feeding index of each parrot species for the community of their food plants and (2) a qualitative supply index of each food plant for the parrot community. The number of plant parts from each exploited plant species was summed to define an interaction index for each parrot species, expressed as $\text{Trophic Interactions}_{\text{parrots}} = \sum_{p=1}^n \sum_{s=1}^n x_{ps}$. This index indicated the extent of the qualitative trophic interaction of each parrot species with the plants present in the ecosystem. For instance, we recorded the use of a variable number of plant parts (categorized as stated above) by *A. rubrogenys*, ranging from 1 (e.g., immature seeds of *Parkinsonia praecox*) to 3 (e.g., mature and immature seeds and flower buds of *Schinopsis marginata*), totaling 28 trophic interactions on 19 plant species (Table 1). Overall, this index ranged between 2 (mature and immature seeds of *S. marginata*) for *A. leucophthalmus* and 108 (multiple plant parts of 52 plant species) for *T. acuticaudatus* (Table 1).

We also computed an interaction index for each plant species exploited by the community of parrots, defined as $\text{Trophic Interactions}_{\text{plants}} = \sum_{p=1}^n \sum_{x=1}^n s_{px}$. This index indicated the comparative importance of each plant species as a supplier of different kinds of food (i.e., plant parts exploited) for the whole parrot community and ranged from 1 for *Tara spinosa* (whose immature seeds were only consumed by *Psittacara mitratus*) to 26 for *Psidium guajava* (whose ripe fruits [pulp], unripe fruits, mature seeds, and immature seeds were consumed by 6, 7, 6, and 7 parrot species, respectively) (see Table S2).

We also evaluated whether the number of Trophic Interactions_{plants} varied between growth forms, pooled into four major plant types (trees, shrubs, climbers and herbs, excluding cultivated herbs and exotic trees) and fruit types (dry or fleshy). If parrots have a pervasive impact on the ecosystem as linkers in multiple processes, we should expect an increasing interaction index with the dominance of plant growth forms, especially with woody plants (trees and shrubs) representing a major proportion of forest biomass (Navarro and Maldonado 2002; López 2003). In addition, as the advantages of seed dispersal appear to have played a key role in the evolution of fruit pulp as a reward to animals moving the seeds in exchange (Fleming and Kress 2013), we also expected a higher interaction index for fleshy fruited than dry-fruited plants. We also assessed whether the food plants of parrots represent a major proportion of the dominant woody plants in the ecosystem, by comparing the number of tree and shrub taxa exploited with that present in the ecosystem according to floristic inventories (Jardim et al. 2003; Atahuachi-Burgos et al. 2005) completed with our own observations of species not covered therein.

Mutualistic interactions: rationale

The diverse foraging methods used by parrots to access the wide array of plant structures on which they feed makes likely the existence of multiple mutualistic interactions with their food plants. First, we considered that parrots feeding on nectar and pollen can contribute, at least marginally, to legitimate pollination of their food plants. Parrots can consume flowers destructively in some species, but not in others (Ragusa-Netto 2002; da Silva 2013). However, even when parrots partially destruct some flowers, they can transport pollen to other flowers that are only tasted or used nondestructively, especially due to the typical pattern of parrot visitation to multiple flowers on the same or different plants exploited sequentially during their daily movements for tracking seasonally synchronized flowering and other resources (Ragusa-Netto 2002; da Silva 2013). Second, we considered that parrots acted as primary seed dispersers of their food plants when they were observed departing from food plants with entire ripe fruits or mature seeds in the beak or feet and subsequently spitting out the items in flight or at another perch (i.e., stomatocory) at a variable distance from the parent plant (Boehning-Gaese et al. 1999; Tella et al. 2015). Tiny seeds (<2 mm diameter) embedded in the slippery pulp of fleshy fruits (e.g., of Cactaceae) may be swallowed by parrots and pass intact through the gut into the feces, thus actually or potentially contributing to primary dispersal by endozoochory (Oliveira et al. 2012; Young et al. 2012). However, this was

not computed as a confirmed mutualistic (dispersal) interaction in this study because we did not search for the presence of viable seeds in parrot feces. Third, parrots may waste entire ripe fruits and mature seeds beneath fruiting plants (Symes and Perrin 2003), thus making them accessible to potential secondary seed-dispersing vertebrates such as birds and mammals, and invertebrates such as ants. Fourth, we considered that by feeding on noxious invertebrates (e.g., lepidopteran caterpillars), parrots may protect and heal their food plants, thus contributing to enhancing their health.

To assess the extent of the mutualistic interactions between parrots and their food plants, we determined whether each plant species (*s*) potentially benefited from each mutualistic interaction (*m*) with each parrot species (*x*), considering (*m*₁) pollination, (*m*₂) primary dispersal at a distance away from food plants by stomatocory, (*m*₃) dispersal beneath food plants implying the potential subsequent dispersal by abiotic factors and the secondary dispersal by other organisms, and (*m*₄) healing, as defined above. With these data, we computed the number of mutualistic interactions for each parrot species, expressed as Mutualistic Interactions_{parrots} = $\sum_{m=1}^n \sum_{s=1}^n x_{ms}$. This index denotes the extent of the qualitative mutualistic interaction of each parrot species with their food plants and ranged between 2 in *P. maximiliani* (i.e., healing *Browningia caineana* and facilitating mature seeds of *P. guajava* to secondary dispersers) and 41 in *T. acuticaudatus* (different mutualistic services to multiple plant species) (Table 1). In addition, an overall index of plant mutualistic interaction for each food plant was defined as Mutualistic Interactions_{plants} = $\sum_{m=1}^n \sum_{x=1}^n s_{mx}$. This index represented the qualitative extent of the mutualistic “services” provided by the parrot community to each plant species, ranging from 0 in several species (no mutualistic function provided by parrots) to 10 in *Prosopis alba* (different services provided by five parrot species) (Table S2).

Data analysis

Factors affecting the provision of plant resources and the mutualistic functions provided by parrots on their food plants were analyzed by GLM using a Poisson distribution with a log-link function for count data. Because it is not possible to infer causality between the mutually influencing indexes considered to characterize species strength, qualitative supply of plant resources, parrot mutualistic functions, and abundance and dominance in the ecosystem, we used nonparametric Spearman rank correlation coefficients to assess the sign and extent of the association between these not normally distributed variables.

Results

Parrots in the frugivore community

Nine parrot species were regularly observed at similar relative abundances between the breeding and nonbreeding season ($r_s = 0.933$, $P < 0.0001$, $n = 9$), and thus, we pooled all seasonal data for subsequent analyses (Table 1). Relative abundances were corrected for species-specific detection probabilities to transform them into density and biomass values (Table 1). A single species of tinamou (Tinamidae) and one of guan (Cracidae) were recorded at values orders of magnitude lower than parrots (Table 1). Therefore, parrots constituted the most dominant guild of large frugivores in terms of abundance, density, and biomass throughout the year.

Food plants and resources exploited

A total of 22,287 parrots were recorded in 1359 feeding bouts on 113 plant taxa belonging to 38 families (Table 1, Table S2). Parrots exploited a diverse array of plants and most growth forms, including trees, treelets, shrubs, cacti, vines, lianas, and epiphytes including hemiparasites, wild and cultivated herbs, and a fern (*Selaginella sellowii*), obtained in all vertical strata (overground, understory, subcanopy, canopy) in the ecosystem. Most food plants were native, including many endemic species. A low proportion of cultivated native and exotic trees (3.5% and 8.8%, respectively, $n = 57$), exotic shrubs (3.6%, $n = 28$, i.e., *Ricinus communis*), and herbaceous cultures (31.8%, $n = 22$) were exploited; all exploited climber species ($n = 6$) were native. The number of plant species exploited varied among parrot species (GLM Poisson error, log-link function, Wald $\chi^2 = 36.22$, $P < 0.0001$), but not seasonally (breeding vs. nonbreeding season, $\chi^2 = 1.21$, $P = 0.27$) or with the number of foraging individuals recorded per species ($\chi^2 = 0.81$, $P = 0.37$).

Exploited plants included a major proportion of the native dominant woody plants in the ecosystem, especially most of tree species present (76.5%, 52 of 68 tree species, see Table S2) and a much lower proportion of shrub species (31.8%, 27 of 85 shrub species). The proportion of exploited taxa for other growth forms (climbers and herbs) was not obtained because of their lack of complete floristic inventories. In any case, the high species richness of these growth forms in the ecosystem was apparently not mirrored by a proportional use by parrots, as shown by the comparatively low number of taxa exploited (i.e., six species of climbers and 15 species of herbs, see Table S2).

The use of the different growth forms, grouped in five major types, showed a main pattern indicating that

arboreal plants were the growth form most exploited by parrot species, except for *Psilopsiagon aymara*, which exploited a higher number of shrubs and wild herbs than trees (Fig. 2A). Only *T. acuticaudatus* and *P. aymara* foraged on all considered growth forms (Fig. 2A).

The resources exploited included fleshy and dry, simple and aggregate, and ripe and unripe fruits of a high variety of structural types (e.g., drupe, legume, nut, samara, berry, etc.), presentation, and colors, as well as their mature and immature seeds. Parrots also fed on most other plant organs and structures (grouped into five major food types), with a main pattern indicating that seeds were the resource exploited from more plant taxa by the most parrot species, except by *P. aymara*, which instead consumed flowers from a higher number of plants (Fig. 2B).

Mutualistic services of parrots to their food plants

The mutualistic services yielded by parrots to their food plants were primarily in the form of seed dispersal, especially by wasting ripe fruits and their seeds beneath fruiting plants (Fig. 3). An unquantified proportion of mature seeds from fleshy fruits wasted beneath parent plants was partially or completely defleshed by parrots, thus enhancing primary dispersal by abiotic factors (wind, runoff water) or by gravity, with seeds rolling variable distances (e.g., spherical seeds of *Anisocapparis speciosa* and *Jatropha hieronymii* rolling several meters from the mother plants after being defleshed by *A. rubrogenys*). Wasted mature seeds can also be secondarily dispersed by other organisms (Fig. 3). We opportunistically recorded the presence of apparently viable seeds of *Ziziphus mistol* and *A. speciosa* in the feces of carnivorous mammals (*G. vitata*, *C. thous*), as well as those of *Celtis ehrenbergiana*, *Capparicordis tweediana*, *P. praecox*, *Prosopis kuntzei*, *P. alba*, *Vachellia aroma*, and *Z. mistol* in feces of free-ranging livestock. In addition, we observed the secondary dispersal by unidentified ants of mature seeds of *Condalia buxifolia* wasted by *T. acuticaudatus*.

Five parrot species were recorded transporting the entire ripe fruits and/or the mature seeds of 15 plant species in their beak or feet while flying (Table 2), thus with a chance of effective primary seed dispersal by stomatochory. Dispersed seeds were mostly from plants with fleshy fruits, but also with dry fruits primarily dispersed by wind and explosive dehiscence (Table 2), moved variable distances away from the parent plants (mean \pm SD = 38.9 ± 76.1 m, $n = 33$, range = 1–400 m, pooling all records for all plant and parrot species, see Table 2 for details). The size (mean \pm SD) of the fruits and seeds of the plant species dispersed by stomatochory

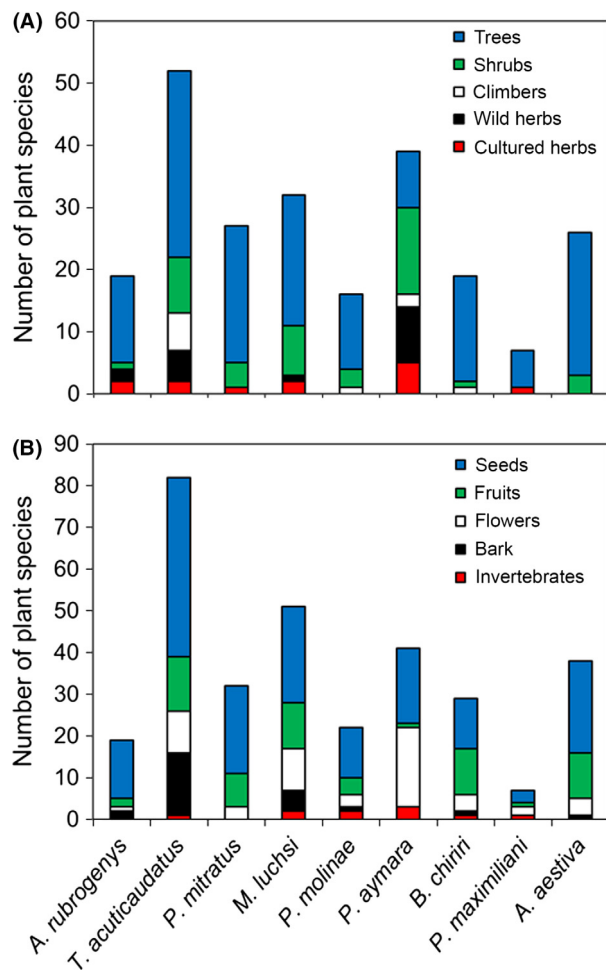


Figure 2. Number of plant species exploited by parrots according to (A) growth forms and (B) resources extracted.

(fruit length = 60.9 ± 56.2 mm, fruit diameter = 18.5 ± 13.8 mm, seed length = 9.1 ± 5.7 mm, seed diameter = 5.9 ± 4.3 mm, $n = 15$ species, Table 2) was not related to the average distance moved ($r_s < 0.33$, all $P > 0.24$ in all cases, $n = 15$). Tiny seeds of fleshy fruits could be primarily dispersed long distances by several parrots species (Table 2) by endozoochory if they were defecated intact, requiring further research, and also by epizoochory through external adhesion to the beak, feet, and feathers (pers. obs.). Thus, different tiny seeds of particular fleshy fruits can be simultaneously moved by several primary dispersal methods during single feeding bouts (e.g., *P. guajava*, Table 2).

Three species of parrots were observed feeding on nectar and pollen, and therefore, potentially pollinating at least 4 of 52 species of native trees (7.7%, *A. speciosa*, *Erythrina falcata*, *Inga adenophylla*, *Ceiba* sp.) (Fig. 3). An apparently strong mutualistic association between *E. falcata* providing nectar and pollen in exchange for pollination services by

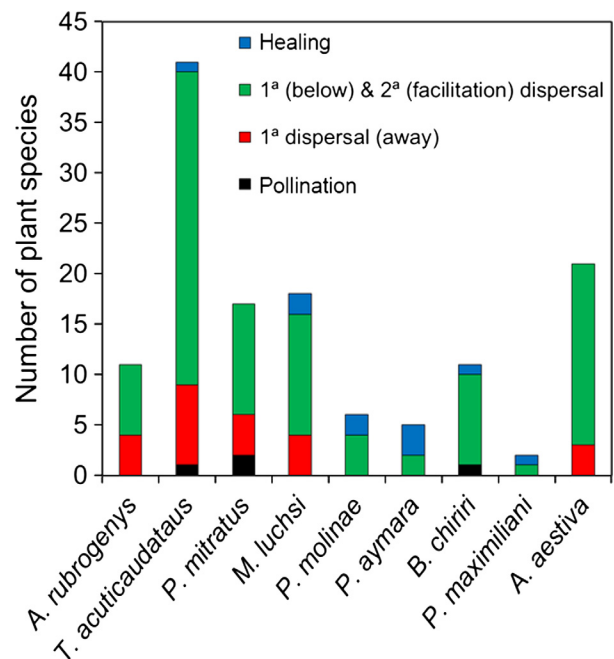


Figure 3. Number of plant species to which parrots from the dry forest of the Bolivian inter-Andean valleys returned each type of mutualist service.

P. mitratus without damaging flowers is notable, as it was repeatedly recorded (13 feeding bouts on different trees involving 388 individuals).

Finally, five parrot species were observed intensively feeding on caterpillars and pupae of leaf-punching microlepidopterans of the Gelechiidae family on three tree species (*Brotogeris chiriri* on *Loxopterygium grisebachii*; *T. acuticaudatus*, *P. aymara* and *P. molinae* on *S. marginata*; *P. aymara* and *M. luchi* on *P. alba*), thus contributing to tree health through the control of these noxious invertebrates. This healing function often involved intensive parrot activity on infested tree patches. For instance, we recorded instantaneous feeding bouts ($n = 8$ and $n = 2$), totaling 223 *M. luchi* and 19 *P. aymara* individuals intensively harvesting caterpillars and pupae in an area where most trees (*P. alba*) sampled (99.2%, $n = 130$) suffered a severe plague by leaf punchers (*Polihymno* sp., Gelechiidae). Additionally, four parrot species (*M. luchi*, *P. aymara*, *P. molinae*, and *P. maximiliani*) were recorded seeking and consuming larvae of unidentified insects on sick cacti of the species *Browningia caineana*.

A total of 472 types of foraging interactions were recorded after considering the different parts of each plant that each parrot species exploited (Table 2). Most interactions corresponded to native species (91.7%, $n = 433$ foraging interactions), while the remaining interactions corresponded to cultivated herbs and exotic plants

that were excluded in the subsequent analyses. The number of different types of foraging interactions varied among parrot species (Trophic Interactions_{parrots}, Wald $\chi^2 = 64.89$, $P < 0.0001$) and seasonal periods (breeding vs. nonbreeding season, $\chi^2 = 8.25$, $P = 0.004$), but was independent on the number of foraging individuals recorded per species ($\chi^2 = 0.01$, $P = 0.91$). As a consequence of these multiple foraging interactions, 132 types of mutualistic interactions were recorded as a whole by summing the different functions provided to each plant species by each parrot species (Table 2).

Influence of trophic and mutualistic interactions on ecosystem properties

Species strength, considering the quantitative interaction of each parrot species with their food plants independently of the plant part exploited (Table 1), was positively related to the density of each parrot species in the ecosystem ($r_s = 0.70$, $P = 0.036$, $n = 9$, Fig. 4). Similar results were obtained for relative abundance and biomass, though they were marginally significant ($r_s = 0.65$, $P = 0.058$ and $r_s = 0.58$, $P = 0.099$, respectively, $n = 9$) due to the apparent outlier species strength of *P. ayмара*, the smallest species in the parrot community (Table 1, Fig. 4; excluding this species, relative abundance, density, and biomass were significantly related to species strength, all $r_s > 0.83$, all $P < 0.01$, $n = 8$). This species showed higher interaction strength than expected from its density (Fig. 4), abundance, and biomass, which supports its specialization on flowers of herbs and shrubs from the understory, in contrast with the trophic pattern based on fruits of trees in the remaining species (Fig. 2).

The comparative importance in qualitative terms of each plant species as suppliers of different kinds of food for the parrot community was higher for woody plants, especially large trees and cacti that represented a major proportion of forest biomass (Trophic Interactions_{plants}, Wald $\chi^2 = 49.19$, $P < 0.0001$, $df = 3$, Fig. 5A). As expected, a higher number of Trophic Interactions_{plants} was also found for fleshy fruited plants when compared with dry-fruited plants (Wald $\chi^2 = 18.10$, $P < 0.0001$, $df = 1$ Fig. 5A).

Overall, the number of mutualistic services yielded by parrots for each of their food plants (Mutualistic Interactions_{plants}) was positively related to the number of different kinds of food extracted from them (Trophic Interactions_{plants}, $r_s = 0.712$, $P < 0.0001$, $n = 100$, Fig. 5B; similar results were found when the analysis was restricted to trees, $r_s = 0.760$, $P < 0.0001$, $n = 52$, and shrubs, $r_s = 0.653$, $P < 0.0001$, $n = 27$). In addition, the number of mutualistic functions provided by each parrot species to their food plants was positively related to the species-specific parrot abundance ($r_s = 0.711$, $P = 0.032$, $n = 9$),

density ($r_s = 0.611$, $P = 0.081$, $n = 9$) and biomass ($r_s = 0.870$, $P = 0.002$, $n = 9$, Fig. 5C) in the ecosystem.

The use and qualitative extent of mutualistic functions provided by parrots increased with the dominance index of each woody plant species in the ecosystem (fixed factor with three levels: 0 = unused plants, 1 = plants used without mutualistic services by parrots, 2 = plants receiving one or more mutualistic functions, Wald $\chi^2 = 18.09$, $P < 0.0001$, $df = 2$, Fig. 6A). The plant dominance index was higher for shrubs than trees (Wald $\chi^2 = 4.51$, $P = 0.034$, $df = 1$, Fig. 6A), but did not differ depending on fruit type (fleshy or dry, Wald $\chi^2 = 1.01$, $P = 0.32$, $df = 1$, Fig. 6A). When the analysis was restricted to woody plants on which parrots exert at least one mutualistic function, the plant dominance index increased significantly with the number of mutualistic functions provided by parrots ($r_s = 0.333$, $P = 0.022$, $n = 47$, Fig. 6B).

Discussion

Parrots as trophic super-generalists

While the number of species and parts of the plant consumed varied among parrot species in the study area, the whole parrot community exploited a high diversity of plants (113 species) across a wide phylogenetic spectrum (38 families), including plants differing in growth habits (from trees to herbs), phenology, type, biomass, and rewards provided in all vertical strata (from canopy to ground). Strikingly, up to 472 foraging interactions were observed when considering the different parts of the plants (and plant-eating invertebrates) consumed. Therefore, parrots interact with their food plants in a much more heterogeneous way than other frugivorous vertebrates. As trophic generalists (for other ecosystems, see Ragusa-Netto and Fecchio 2006; Gilardi and Toft 2012; Lee *et al.* 2014), parrots may have a pervasive impact on the vital cycles of their food plants through a wide range of interactions across an antagonism–mutualism gradient (Gilbert 1980). In fact, it has been suggested that parrots are linked to the evolution of masting strategies exerting a regulatory role in forest dynamics due to their role as seed predators (Galetti and Rodrigues 1992; Boyes and Perrin 2010; Villaseñor-Sánchez *et al.* 2010). However, the potential role of parrots as super-generalist frugivores involved in multiple mutualistic interactions with their food plants has been largely overlooked.

Mutualistic interactions between parrots and their food plants

We recorded up to 132 types of mutualistic interactions of parrots with their native food plants. This is indeed a

Table 2. Features of plants actively or potentially dispersed by stomatochory and endozoochory, respectively. Mean \pm SD distances of stomatochory dispersal are shown according to each disperser parrot species (*A.r* = *Ara rubrogenys*, *T.a* = *Thectocercus acuticaudatus*, *Ps.m* = *Psittacara mitratus*, *M.l* = *Myopsitta luchi*, *Py.m* = *Pyrrhura molinae*; *B.ch* = *Brotogeris chiriri*, *P.m* = *Pionus maximiliani*).

Species	Fruit type, color/growth form	Putative dispersal	Fruit-seed size, mm	Number of seeds	Disperser species and dispersal distance (m)
Stomatochory					
Anacardiaceae					
<i>Schinopsis marginata</i>	Dry, yellow-red/tree	Wind	28 \times 8–3.5 \times 3	1 (1)	<i>T.a</i> (40)
Cannabaceae					
<i>Celtis ehrenbergiana</i>	Fleshy, yellow/tree	Animals	6 \times 6–2.5 \times 1.5	1 (1)	<i>T.a</i> (1)
Apocynaceae					
<i>Vallesia glabra</i>	Fleshy, white/shrub	Animals	10 \times 4–6 \times 2	1 (1)	<i>M.l</i> (2)
Capparidaceae					
<i>Anisocapparis speciosa</i>	Fleshy, green/tree	Animals	59 \times 58–18 \times 16	4 (2–6)	<i>A.r</i> (35), <i>A.a</i> (3)
<i>Capparicordis tweediana</i>	Fleshy, light green/shrub	Animals	15 \times 15–4 \times 4	3 (2–4)	<i>Ps.m</i> (8), <i>A.a</i> (3)
<i>Cynophalla retusa</i>	Dry, green/tree	Animals	124 \times 13–11 \times 5	8 (2–23)	<i>Ps.m</i> (6 \pm 4, <i>n</i> = 2)
Euphorbiaceae					
<i>Cnidocolus</i> spp.	Dry, green/shrub	Explosive deh.	16 \times 12–12 \times 4	3 (2–3)	<i>T.a</i> (25 \pm 7, <i>n</i> = 2), <i>Ps.m</i> (8)
<i>Jatropha hieronymii</i>	Dry, light green/shrub	Explosive deh.	25 \times 24–15 \times 8	3 (3)	<i>A.r</i> (76 \pm 65, <i>n</i> = 7), <i>T.a</i> (10)
Fabaceae					
<i>Inga feuillei</i>	Fleshy, green-brown/tree	Animals	160 \times 20–20 \times 15	7 (4–14)	<i>T.a</i> (5)
<i>Parkinsonia praecox</i>	Dry, brown/tree	Animals	57 \times 14–11 \times 5	2 (1–3)	<i>T.a</i> (1)
<i>Prosopis kuntzei</i>	Fleshy, brown-black/tree	Animals	137 \times 20–12 \times 8	11 (6–16)	<i>A.r</i> (30)
<i>Prosopis alba</i>	Fleshy, yellow/tree	Animals	163 \times 10–7 \times 5	21 (11–29)	<i>A.r</i> (400), <i>T.a</i> (40), <i>M.l</i> (10 \pm 0, <i>n</i> = 2), <i>A.a</i> (150)
<i>Senegalia gilliesii</i>	Fleshy, brown/shrub	Animals	56 \times 21–8 \times 7	4 (2–6)	<i>M.l</i> (2)
Myricaceae					
<i>Psidium guajava</i>	Fleshy, yellow/tree	Animals	38 \times 38–1.5 \times 1.5	≥ 50	<i>Ps.m</i> (100), <i>M.l</i> (28 \pm 18, <i>n</i> = 2)
Sapindaceae					
<i>Serjania</i> spp.	Dry, red/vine	Wind	20 \times 15–5 \times 4	3 (3)	<i>T.a</i> (5)
Endozoochory (potential)					
Cactaceae					
<i>Browningia caineana</i>	Fleshy, yellow-green/cacti	Animals	30 \times 30–1 \times 0.6	≥ 50	<i>M.l</i>
<i>Cereus</i> spp.	Fleshy, red/cacti	Animals	72 \times 50–1.5 \times 1.5	≥ 50	<i>T.a</i> , <i>M.l</i> , <i>B.ch</i> , <i>A.a</i>
<i>Harrisia tetraacantha</i>	Fleshy, reddish-green/cacti	Animals	55 \times 40–1.5 \times 1.5	≥ 50	<i>T.a</i> , <i>Ps.m</i> , <i>M.l</i> , <i>Py.m</i> , <i>B.ch</i> , <i>A.a</i>
<i>Neoraimondia herzogiana</i>	Fleshy, light brown/cacti	Animals	50 \times 50–1 \times 1	≥ 50	<i>T.a</i> , <i>A.a</i> , <i>M.l</i> , <i>B.ch</i>
Moraceae					
<i>Ficus carica</i>	Fleshy, green-violet/tree	Animals	55 \times 40–0.5 \times 0.5	≥ 50	<i>M.l</i> , <i>B.ch</i>
<i>Maclura tictoria</i>	Fleshy, brown/tree	Animals	20 \times 12–2.2 \times 1.3	≥ 50	<i>Py.m</i> , <i>B.ch</i>
Myricaceae					
<i>Psidium guajava</i>	Fleshy, yellow/tree	Animals	38 \times 38–1.5 \times 1.5	≥ 50	<i>T.a</i> , <i>Ps.m</i> , <i>M.l</i> , <i>Py.m</i> , <i>B.ch</i> , <i>P.m</i> , <i>A.a</i>

conservative result. First, despite our intensive survey (>22,000 foraging parrots observed across two annual cycles) and the fact that the number of plant species consumed and number of foraging interactions were not related to the number of foraging individuals observed per species (thus suggesting interactions were not largely underestimated for the less abundant parrot species), it would be presumptuous to say we observed all foraging and mutualistic interactions.

The wide flowering phenology of plants in the study area resulted in a number of missed flowering events and thus additional potential pollination interactions. Our approach was conservative, as we only reported as

pollination function those cases on plant species on which we observed parrots feeding on pollen and nectar, not other floral structures implying its destruction. Of course, it could be crucial to provide detailed data on the actual role of parrots as pollinators in regions others than Australasia, which requires specific research. Tree healing by preying on noxious invertebrates was observed by six of the nine parrot species studied, but they were more evident when we fortuitously encountered local insect-plague events. Thus, additional field research may increase the opportunity to observe additional tree healing interactions. Parrots' consumption of invertebrates differs in form and frequency from insectivorous birds seasonally

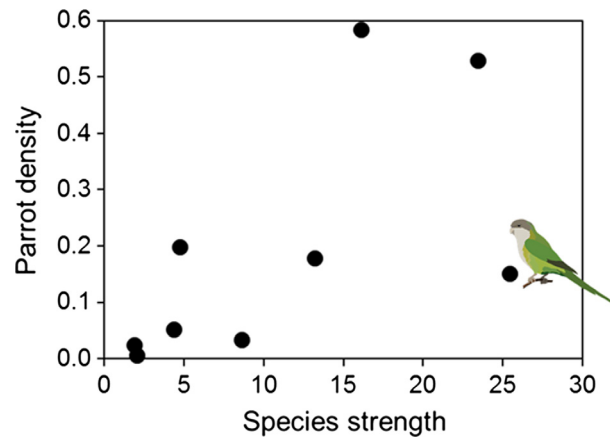


Figure 4. Relationships between species-specific parrot density (indv./10 ha) and interaction (species) strength with their food plants. The apparently higher species strength than expected from its density of *Psilopsiagon aymara*, the smallest species in the parrot community, is remarkable.

feeding on fruits. As primarily insectivorous birds exploit fruit pulp rather than seeds, they generally forage on ripe fruit only available late in the fruiting season (Jordano 1995, 2000). Parrots feed on ripe and unripe seeds and fruit (pulp) as well as on other plant structures, thus behaving as generalist consumers of vegetal matter. The invertebrate consumption by parrots seems primarily directed toward temporal plant pests concentrating abundant food, although they also feed on invertebrates at lower abundances. Thus, parrots differ from primarily insectivorous birds in behaving as opportunistic insectivorous focusing on large ephemeral food pulses represented by plant plagues. By focusing on these plants pests, the balance between the costs of collecting small prey can be compensated by the benefits of obtaining highly nutritive proteinaceous food at high spatiotemporal concentrations. In this sense, their function in plant healing may be more accused than that from smaller and less abundant passerines, at least in the studied ecosystem. Second, we were not able to confirm endozoochory as we could not collect parrot feces for this study. However, we observed seven parrot species feeding on fruits of seven plant species,

whose tiny seeds were apparently swallowed intact embedded in pulp. Previous works have shown that these small seeds can be subsequently defecated by different

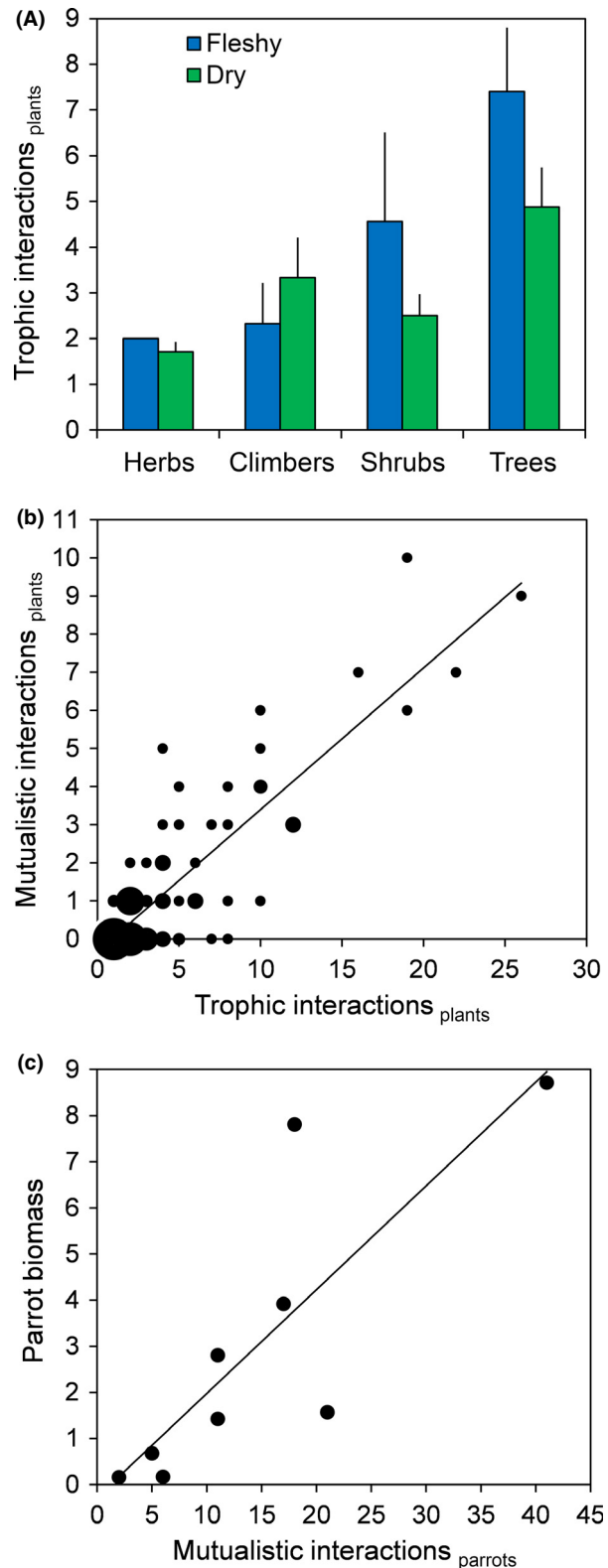


Figure 5. (A) Mean \pm SE number of different kinds of resources exploited by the parrot community (Trophic Interactions_{plants}), according to growth form and fruit type of their food plants. (B) Relationship between the number of mutualistic services provided by the parrot community to each of their food plants (Mutualistic Interactions_{plants}) and the different kinds of food extracted from them (Trophic Interactions_{plants}). (C) Relationships between the number of mutualistic functions provided by each parrot species to their food plants (Mutualistic Interactions_{parrots}) and the species-specific parrot biomass (kg/km²). Regression lines of the correlations were shown for graphical representation of trends.

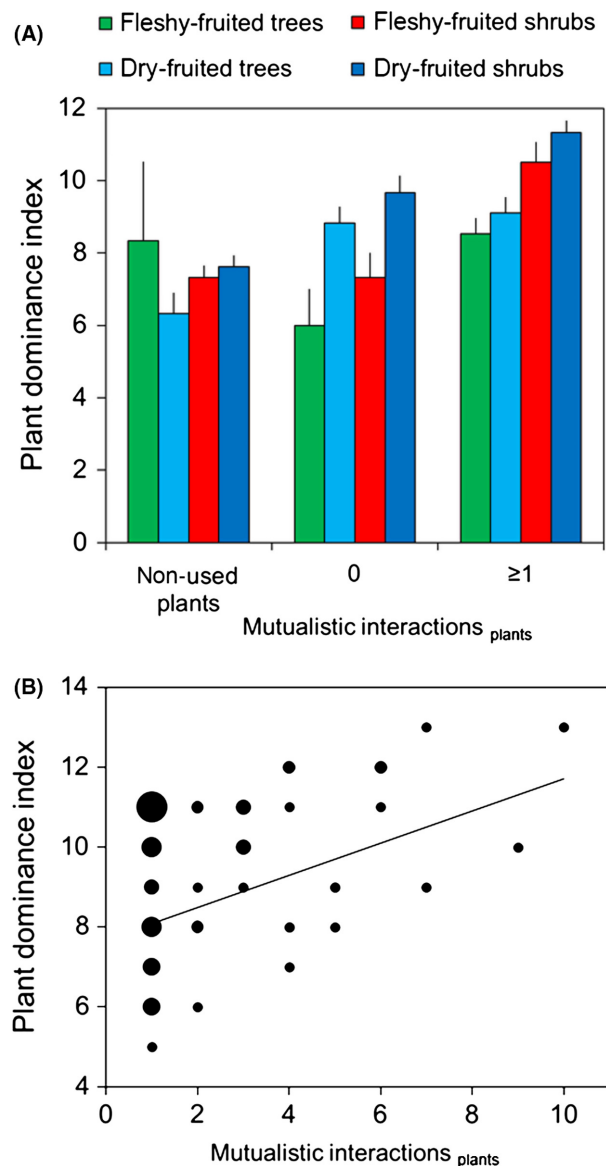


Figure 6. (A) Mean \pm SE dominance index of woody plant species (trees and shrubs) in the Bolivian inter-Andean valleys ecosystem according to growth form, fruit type, and use and extent of mutualistic functions provided by parrots to their food plants (Mutualistic Interactions_{plants}). (B) Relationship between the plant dominance index and the number of mutualistic functions provided by parrots to their food plants (Mutualistic Interactions_{plants}) when the analysis was restricted to woody plants on which parrots exert at least one mutualistic function. Regression line of the correlation was shown for graphical representation of the trend.

parrot species without losing germination capability (Fleming *et al.* 1985; Oliveira *et al.* 2012), and thus, our observations could correspond to legitimate endozoochory but, conservatively, were not computed as mutualistic interactions.

Our records of stomatochory merit a special mention. As part of the typical foraging behavior of parrots, five species were recorded carrying fruits to distant perches (up to 400 m) and eventually dropping them, thus dispersing seeds with a possibility of establishing seedlings. Germination of seeds transported by parrots has been recently confirmed in other biomes, even when seeds were partially consumed by parrots (authors' unpublished data). In this study, a majority of the seeds dispersed corresponded to plants with fleshy fruits, as expected from the dispersal advantages leading to the evolution of such fruits, which are generally moved when consumed by animals (Fleming and Kress 2013). Strikingly, parrots were also recorded moving seeds of plants putatively dispersed by wind, gravity, and explosive dehiscence. This implies that parrots can disperse these plants to microhabitats and distances other than those expected by the above-mentioned major dispersal mechanisms, with pervasive population- and community-level implications. Stomatochory also implies that parrots can disperse fruits and seeds larger than those dispersed by endozoochory, which is constrained by gape size (Wheelwright 1985), thus potentially leading to the evolution of large fruits and seeds in their food plants. In fact, the mean size of fruits and seeds dispersed through stomatochory was higher than that reported for other birds and similar to those dispersed by mammals (Jordano 1995; Fleming and Kress 2013). Moreover, the typical wasteful feeding of parrots promoted an abundant "rain" of entire ripe fruits and mature seeds from the canopy, facilitating food availability for secondary dispersing organisms. Although this activity can be perceived without a direct and important benefit for plants, it needs adequate testing. We have provided evidence summing to that found in the literature that this wasting activity may promote secondary dispersal, which has been highlighted as more important than previously thought, for instance by scatter-hoarding animals (Norconk *et al.* 1998; Vander Wall *et al.* 2005). A particularity of this parrot activity is the high amount of intact seeds that they can drop in single feeding bouts, thus causing the accumulation of mature seeds below the fruiting trees (Symes and Perrin 2003). This can swamp predators and thus promote hoarding-derived dispersal by these predators (Kelly and Sork 2002). In any case, this potential benefit for plants was the most frequently observed because it is more easily recorded than other interactions, especially dispersal by stomatochory requiring intensive observations of particular individuals. Fruit handling by parrots, including defleshing, seed scratching, and scarring, may also presumably play a role in gravity dispersal (e.g., by rolling), survival, and germination of undamaged seeds, as reported for other dispersers (Norconk *et al.* 1998). Regarding the simpler role of gravity

making seeds available to secondary dispersers, parrots make a difference. First, their action frequently dropping ripe and close to ripening fruits and seeds is scaled in time compared to the action of gravity, which is concentrated at the very end of the fruiting period, thus making seeds available on the ground for a much longer time period at the scale of both individual and plant populations. Second, in some of the studied plant species (e.g., *S. marginata*), a high proportion of fruits become dry before falling by gravity, while parrots drop to the ground high amounts of mature seeds before they become unviable.

Although dispersal and predation of seeds have been generally considered the primary determinants of population dynamics structuring plant communities, their relative importance can vary widely depending on the conditional impact of the community of plant antagonists and mutualists, as well as on multiple species-specific traits under spatiotemporally variable environmental conditions (Howe and Miriti 2004; Vander Wall *et al.* 2005; Schupp *et al.* 2010). Indeed, even strong seed predation and low seed dispersal may have relatively low effects on plant recruitment in long-living plants owing to massive crops and mast seeding, swamping predators (Kelly and Sork 2002). Moreover, our unpublished observations on this and other parrot communities indicate that foraging parrot flocks often move between fruiting trees before fully harvesting them, thus reducing the impact on the fitness of individual plants. Meanwhile, other factors such as pollination limitation and pest impact can exert primary influences on plant demography and population dynamics (Wang and Smith 2002; Koenig and Ashley 2003). Overall, the large number of seeds that parrots handle, waste, and transport daily, plus the abundance and the high daily and seasonal mobility of these strong flyers, suggest that they are central dispersal agents for most plant species in the studied ecosystem (see also Young *et al.* 2012 for alpine flora), despite the high proportion of flowers and seeds that are predated. Parrots may even be the only effective dispersers of the large seeds of several of the dominant plants in the dry forest of the Bolivian inter-Andean valleys, where no other large recognized avian frugivores (e.g., toucans, trogons), primates, or squirrels live (Anderson 1997; Kissling *et al.* 2009) or, when present, occur at comparatively very low abundances (e.g., tinamous and guans). Parrots also provided the natural control of invertebrate pests of their food plants (e.g., Greene 1998), and acted as potential pollinators of a similar proportion of woody plants as that recorded for whole bird assemblages in several wet tropical regions (Devy and Davidar 2003; Fleming and Kress 2013). Thus, parrots yielded multiple high-quality and high-quantity services, directly and/or indirectly, to

the wide array of their food plants and could therefore be considered keystone mutualists with a pervasive impact in plant assemblages.

Missing and overlooked links

Flowering and fruiting phenological patterns often result in a spatiotemporally heterogeneous mosaic of plant resource predictability and supply promoting daily and seasonal movements of parrots tracking food abundance and nutritional features (e.g., Renton 2001; Moegenburg and Levey 2003). This, together with the high variety of exploited resources, suggests that our extensive sampling may have missed a proportion of the potential pairwise parrot–plant taxa interactions (see above), especially those involving the different parts of each plant that each parrot species can exploit. Obviously, a proportion of interspecific interactions remained unobserved because they are extremely rare or difficult to detect (missing links) or hardly possible (forbidden links) due to biological constraints such as spatiotemporal uncoupling and size mismatching (Bascompte and Jordano 2014).

In addition, links not considered or eventually excluded from the research can also potentially involve abundant species with a high probability of multispecific interactions but contribute to particular linkages in an unappreciated fashion and frequency. These types of disregarded interactions (and actors), here called “overlooked links” (and linkers), may have passed unnoticed, been nonevident or not entirely understood, and assumed to be residual and/or negligible. As a consequence, they often become relegated to particular research domains and excluded from others based on old, partial, or dogmatic observations lacking a comprehensive critical evaluation. Importantly, the missing interactions would likely imply further dispersal mutualisms by each possible seed transport method (typically endozoochory), food facilitation for secondary dispersers, pollination, and population control of noxious organisms. These actually observed and missing links were previously overlooked in studies where parrots were underestimated or even not considered as forming part of mutualistic networks.

Surprisingly, all of the parrot functions that we are reporting were previously recorded for other parrot species elsewhere in the world, but not reported, or scarcely considered, in plant–bird interaction studies. Some parrot species are known to prey on invertebrates (Collar 1997; Juniper and Parr 2010), and some, other than the typically nectarivorous species (i.e., Family Loridae), have been reported to feed on nectar (Collar 1997; Ragusa-Netto 2002; Boyes and Perrin 2010; Juniper and Parr 2010; da Silva 2013). A seminal experiment conducted with a single parakeet (Janzen 1981) may have led to the

propagation of the idea that parrots are not legitimate endozoochorous dispersers. Meanwhile, subsequent findings supporting the germination capability of tiny seeds defecated by parrots (Fleming *et al.* 1985; Oliveira *et al.* 2012), and the potential of a parrot species to act as the primary dispersal agent for entire plant communities through endozoochory (Young *et al.* 2012), have gone overlooked. Stomatochory by parrots has also been previously recorded (Symes and Perrin 2003; Sazima 2008; Tella *et al.* 2015), even as a major dispersal mode with parrots as the sole or primary dispersers of particular species (Boehning-Gaese *et al.* 1999). Observing parrots flying with fruit in the beak or feet from a feeding tree and either dispersing it by spitting it out in flight or at another tree has proven difficult and time-consuming, and this may explain why this likely common behavior has been largely overlooked (Tella *et al.* 2015). As a consequence of the usual focal sampling of individual fruiting plants, this kind of seed dispersal event has been generally unrecorded or unconsidered in studies of seed dispersal by avian frugivores (but see Saavedra *et al.* 2014). Finally, the widespread behavior of parrots wasting large amounts of ripe fruits and their seeds while feeding on fruiting plants has lacked a functional explanation (e.g., Symes and Perrin 2003), but undoubtedly may facilitate both primary and secondary dispersal.

Remarkably, our study recorded all of the above interactions together in a single ecosystem, highlighting the overlooked role of parrots as multilinkers along an antagonism–mutualism gradient that may have pervasive effects on plant communities and ecosystem functioning (see below). We feel further research should be advanced in two ways. First, our qualitative assessment should be complemented with quantitative measurements of all parrot–plant interactions for a better understanding of the functional role of parrots in the studied ecosystem. Second, one could argue that the key role of parrots we are reporting results from studying an ecosystem particularly poor in avian (Kissling *et al.* 2009) and other frugivorous species. Therefore, particular attention should be paid to potential parrot–plant links in other ecosystems before generalizing the mutualistic role of parrots in tropical ecosystems. We expect that a number of overlooked mutualistic interactions will be identified. In fact, stomatochory may be a widespread phenomenon as we have already recorded >600 dispersal events of 94 plant species by 28 parrot species, which were invariably considered previously only as plant antagonists, in a variety of habitats and ecosystems (Tella *et al.* 2015). Finding some of these overlooked links may add key pieces to the mosaic of mutualistic interactions and may change the current perception of the structure, organization, and functioning of some ecological webs. For instance, parrots have been

excluded in ecological network studies, especially in mutualistic networks mediated by pollination and seed dispersal in the tropics (reviewed by Fleming and Kress 2013; Bascompte and Jordano 2014). By including parrots as mutualistic dispersers and pollinators of many of their food plants, the conclusions of these studies could change, with important implications in environmental conservation.

Role of parrots in ecosystem structure and functioning

Viewed under the context of mutualism, interacting organisms can become reciprocal determinants of the distribution, abundance, and demography of their counterparts, hence influencing ecosystem structure and dynamics to a variable extent depending on the functional relevance of the interacting organisms (Hillebrand *et al.* 2007; Anderson *et al.* 2011; Wisz *et al.* 2013). As often reported in plant–animal mutualisms (Vázquez *et al.* 2009), our results showed that interaction frequencies between parrots and their food plants primarily relied on their close functional interdependence, rather than on random encounter frequency according to their abundance. Dominant woody plants representing a major proportion of forest biomass, especially fleshy fruited trees and shrubs, were central suppliers of multiple types of food for the parrot community. As a consequence, the number of complementary and redundant mutualistic functions provided by parrots to each plant species was positively related to the number of different types of food extracted from them, as expected for species playing a key role as mutualists in ecosystems (Vázquez *et al.* 2009).

From an evolutionary perspective, these results suggest a primary role of reciprocal selection with an influence on species-level properties of mutualistic partners (Keddy 1992; Wisz *et al.* 2013). Accordingly, we found that the number of mutualistic functions provided by each parrot species was positively related to the species-specific parrot abundance, density, and biomass. These results suggest that mutualistic plant–parrot interactions can have demographic implications for both interacting partners, thus contributing to the ongoing structure and organization of the ecosystem (Thompson 2005; Wisz *et al.* 2013). This sort of “mutual engineering” was patent because the relative species-poor community of super-generalist parrots represented a numerically and biomass-dominant guild among vertebrate frugivores in the study area, and because they interact mutualistically with most foundation biomass-dominant woody plants in this ecosystem. This pattern is consistent with those obtained from other study systems, showing that common generalist species may be particularly relevant for the structure and

functioning of mutualistic networks and multiple ecosystem processes (Brown *et al.* 2001; Stachowicz 2001; Bruno *et al.* 2003; Vázquez *et al.* 2009; Gaston 2010). Therefore, contemporary species-level traits of both plants and parrots should be central biological attributes of the ecosystem, as a likely ecological consequence of their strong and meaningful co-dependency in evolutionary time.

Interestingly, the use and qualitative extent of mutualistic functions provided by parrots increased with the dominance of each woody plant species in the ecosystem, including both plants used and unused as food by parrots. This relationship was especially patent when woody plants on which parrots exert at least one mutualistic function were considered. This suggests a key role of the strong mutually enhancing interactions on driving properties and functioning of ecological systems through a combination of coevolutionary complementarity, increased fitness outcomes of the interacting partners, and the coevolutionary convergence among super-generalists within the same trophic level (Thompson 2005; Guimarães *et al.* 2011; Nuismer *et al.* 2013). The alternative hypothesis stated that species acting as plant antagonists can also alter the composition and abundance of plant communities by selectively consuming the most palatable or nutritious species, thus bestowing a competitive advantage to those plant species that are avoided or nonpreferred due to their chemical or structural defences (Dearing *et al.* 2005; Iason *et al.* 2012). This hypothesis conflicts with the widespread parrot consumption of seeds and other parts of plant species containing elevated concentrations of secondary compounds (such as phenolics and alkaloids) that are, for most vertebrates, highly toxic and even poisonous (Gilardi and Toft 2012). In fact, according to species strength, several of the most consumed plants (e.g., *Cnidoscolus* sp. and *J. hieronymi*, Euphorbiaceae) show strong structural defences (e.g., stinging hairs) and high concentrations of unpalatable and toxic secondary metabolites (authors' unpubl. data). Other highly toxic species such as *Zanthoxylum coco* (Rutaceae), *Cestrum parqui*, or *Datura ferox* (Solanaceae) were also consumed even by the smaller species, which supports the idea that parrots have a singular tolerance and/or efficient detoxification mechanisms for most phytotoxins (Gilardi and Toft 2012). By foraging on toxic but nutritious plants, parrots exploit a relatively vacant trophic niche while enhancing the populations of these plants by the multiple mutualistic services recorded in this study (e.g., seed dispersal of the euphorbias cited above). Thus, parrots favouring some plant species over others may contribute to competitive exclusion among herbivores mediated by food palatability and/or toxicity, which requires further research for its implications in the structure and functioning of ecosystems.

Overall, our results highlight the interest of integrating trophic webs considering different food types from single plant species, different types of mutualistic services among partners and the structure of plant communities, in order to obtain a more complete and realistic view of plant–animal interactions and their roles driving ecosystem functioning. Ultimately, the net contribution of parrots to the population dynamics of their food plants relies on the balance between the impact on flower and seed predation *versus* the quantitative and qualitative benefits derived from acting as effective genetic linkers, seed facilitators for secondary dispersers, and plant protectors. Thus, the quantitative advantages in the form of mutualist services provided by abundant and mobile parrots could compensate for a qualitative disadvantage derived from their detrimental effects as flower and seed predators. This simultaneous or conditional contribution of parrots as plant antagonists and mutualists depending on the multiple stages of the plant life cycle on which they can exert a relevant influence warrants further research for its potential ecological significance. This requires detailed information on plant demography derived from the activity of parrots. Possible connections among sequential stages along plant reproductive cycles with positive and negative feedbacks on the predictability, abundance, and features of their food resources suggest that parrots have great potential as mediators in trophic and mutualistic networks, with pivotal effects on other ecosystems processes. Because of their comparatively high abundance, variable body size, mobility, and behavioral and ecological plasticity, parrots can act as resource linkers in ecosystem functioning through the flux of energy among different trophic levels within and across ecosystems (Hooper *et al.* 2005; Rietkerk and Van de Koppel 2008). They can induce cascading effects in food webs by facilitating a wide array of plant resources to multiple organisms through their wasting behavior, but also by their effects on the quantity and features of resources extracted from and returned to particular food plant species, populations, and communities and thus on the overall turnover of nutrients in the ecosystem.

The recognition of parrots' influence on plant life cycles and ecosystem functioning warrants multidisciplinary investigations likely providing fruitful research avenues. The prevailing antagonistic view of parrots implies that other less mobile and gape size-constrained frugivore guilds (e.g., fruit gulpers) should play a major role as dispersal mutualists on ecosystem structure and resilience (Markl *et al.* 2012; Fleming and Kress 2013; Galetti *et al.* 2013; Vidal *et al.* 2013), including compensation for the assumed detrimental impacts of parrots on the forest. Therefore, by neglecting parrots as mutualists of their food plants, the role of the generally assumed major vertebrate mutualists on ecosystem functioning and resilience may

have been overestimated. Conversely, the potentially pervasive ecological role of parrots could contribute to the memory and resilience of ecosystems against forest overgrazing and degradation, especially because of their dependence on declining foundation tree species (*sensu* Ellison *et al.* 2005; e.g., Bonadie and Bacon 2000). Therefore, the actual functions and services provided by parrots, whatever they may be in each region and ecosystem, merit investigation before complete disruption by increasing habitat destruction and population declines due to the persecution and capture of parrots for the pet trade (Tella and Hiraldo 2014). New insights from the study of parrot–plant mutualistic networks and its relevance in ecosystem integrity should help to properly identify the extent of ecosystem services lost due to parrot decline and extirpation from the wild.

Acknowledgments

We thank M. de la Riva, E. Pacifico, H. Garrido, A. Requejo, I. Vera, R. Rojas, J. Paca, G. Flores, S. Huici, E. Yucra, and D. Alberto for fieldwork assistance. E. Sebastián-González, A. Montesinos, and P. Jordano greatly helped to improve the manuscript. Funding was provided by Zoo de Barcelona and Biorena (January 2011), Junta de Andalucía (PAI RNM107 to JLT and FH, April–September 2011), Fundación Biodiversidad (2012–2013), Conselho Nacional de Desenvolvimento Científico e Tecnológico (206107/2014-5 to FVD, 2015) and a Severo Ochoa “microproyecto” award (to FH). We acknowledge the efforts of two anonymous reviewers in improving the paper’s content.

Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Histogram of detection distances and the estimated detection function with 95% confidence interval of each parrot species.

Table S1. The 95% maximum detection distances (w), total number of detections and detections within w (in

parenthesis), the number of distance classes for fitting of the detection functions and the average detection probability (P) with 95% confidence intervals of each parrot species.

Table S2. Features of used and unused plants by parrots in the Bolivian inter-Andean valleys. n . observ. and n . indiv. represent the number of parrots flocks and individuals foraging on each plant species.